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FACTORS AFFECTING CONE AND SEED PRODUCTION IN WESTERN REDCEDAR

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ABSTRACT

The pollination mechanism in western redcedar (*Thuja plicata* Donn) is described for containerized clones, based on phenological observations and scanning electron micrographs. The seed cones ended dormancy at the end of February, 1986, opened, exposing the ovules and soon after secreted pollination drops. The rate of cone closure was influenced by the presence of pollen. Unpollinated cones remained open and secreted pollination drops for 10 to 20 days, before the expansion of the bract-scales completely covered the ovules. The presence of pollen accelerated cone closure. The number of pollinated ovules per cone (pollination efficiency) influenced the final size of the cones.

The time of pollination which produced the highest pollination efficiency was just after cone opening, while pollination drops were present but before bract-scale expansion.

The effects of self, cross and no pollinations on filled seed, pollination efficiency, ovule development and seed efficiency were tested on rooted ramets of six western redcedar clones. Ovules must be pollinated with viable pollen and cones must have a minimum of one developing seed before they will develop. The greatest loss of seeds results from a failure of ovules to be pollinated followed by low pollen viability. Unpollinated ovules abort at the megaspore or free nuclear stages. Pollinated ovules may abort at any stage but most commonly during the long free nuclear stage. Selfing had a limited effect on seed set.

The most effective way to increase seed set in western redcedar is to pollinate cones of female parents, having a history of high seed efficiency, several times within a one week peak pollination period with abundant pollen of known high percent viability.

INTRODUCTION

Western redcedar (*Thuja plicata* Donn) is a commercially important conifer native to Alaska, British Columbia, and Pacific Northwest States. It is distributed primarily in coastal regions from southern Alaska to Northern California but also occurs in the interior of British Columbia and to the western slope of the Rocky Mountains into Idaho and Montana where it is confined to regions having abundant precipitation and humidity (Fowells 1965; Hosie 1979). Earlier reports on cone initiation (Owens and Pharis 1971) and pollination, ovule and seed development (Owens and Molder 1980) showed that, although it is a prolific cone producer, seed production per cone is very low, averaging only 2.6 seeds per cone (Owens and Molder 1980). Although each cone contains about 16 ovules at pollination, an average of only 16% of these developed into filled seeds under natural conditions and often many cones contained no filled seed (Owens and Molder 1980). From a recent review of the literature on seed production in forest trees (Owens and Blake 1985) and earlier silvicultural studies (Fowells 1965), it became apparent that the causes for this low seed production were not known.

The low seed efficiency (SEF), defined as the percent of potential seeds (ovules) per cone which develop into mature filled seeds (Bramlett *et al.* 1977), is unacceptable for seed orchards where the goal is maximum production of high quality seed. About 3.19 ha of western redcedar seed orchards have been established by several forest companies (Hanson 1985) in British Columbia, on the Saanich Penninsula near Victoria and Yellow Point near Nanaimo. In order to attain maximum seed production from these orchards, the causes of poor SEF should be determined. These causes may include inadequate pollination, low pollen vigor and viability, and cone, ovule and embryo abortion at various stages of the reproductive cycle (Owens and Blake 1985). In western redcedar it takes about 6 months from pollination in late winter to seed release in late summer in southwestern British Columbia (Owens and Molder 1980, 1984).

In order to investigate these factors and their relative importance to seed production in western redcedar, three studies were done to determine: (1) The role of the pollination mechanism and the effect of the time of pollination on pollination efficiency; (2) The effect of self, cross and no pollination on cone and seed development; and (3) The effect of open pollination and carrying capacity on seed yield.

MATERIALS AND METHODS

Study 1: Three 6 to 7 year-old containerized clones (two ramets per clone) at Western Forest Products' Lost Lake Seed Orchard, Victoria, B.C. were used in the study. In late February 1986, before the seed cones opened, on each of two clones, 6 branches with a minimum of 25 seed cones were isolated using paper pollination bags. All pollen cones were removed from these branches to ensure no contamination. The third clone was left unbagged and monitored and sampled for seed-

cone development. Seed-cone development was divided into five phenological stages: (1) unopened, quiescent cone (Fig. 1); (2) bract-scales reflexed but no pollination drops (Figs. 2, 3); (3) pollination drops present (Figs. 4-8); (4) bract-scales swelling (Fig. 9); and (5) closed cone. Two to 4 seed cones were collected at each phenological stage, mounted on stubs using silver conductive paint and observed immediately with a JEOL-35U scanning electron microscope (SEM) operating at 10 Kv.

Branchlets containing pollen cones were collected from 10 mature trees in a natural stand near Victoria, 2 to 4 days before pollen release. The pollen cones were maintained at room temperature and the pollen collected and bulked as it shed.

Development of the seed cones in the pollination bags was closely monitored and the conelets within one bag per clone were pollinated at different phenological stages with 0.6 ml of a polymix of the freshly collected pollen. Pollen was blown into the bags on different dates (Table 1) using a hypodermic needle fitted to a 0.3-mL chamber attached to a can of compressed air. Additional puffs of air ensured that the pollen cloud was distributed evenly within the pollination bags. Approximately 20 minutes later, after the pollen had settled, the pollination bag was removed and replaced with a new bag to ensure that pollination did not occur during subsequent conelet development. On some pollination dates a large proportion of the cones were equally or nearly equally distributed between 2 stages. When this occurred cones at both stages were pollinated so one pollination date often encompassed two phenological stages (Table 1). Cones at other phenological stages within the bags were removed after pollination, but before the bags were replaced.

Several days after all cones reached stage 5 (cone closure), the pollination bags were replaced with mesh insect bags. The cones were collected in mid-August after the cones had began to dry and turn brown. There was considerable variation in the size of the mature cones. All cones collected per clone and pollination date (phenological stage) were divided into three size classes based on cone length: (1) >1 cm (fully developed cones); (2) 1 cm 0.5 cm (partially developed cones); and, (3) <0.5 cm (underdeveloped cones).

Up to 20 cones per clone, pollination date and size class were randomly selected. The seeds removed from each cone were divided into 3 seed classes; (1) full-sized round seed, (2) flat and partially developed seed, and (3) small, underdeveloped seed (Fig. 10a, b, c). To determine the number of filled seed per cone all class 1 and 2 seeds were radiographed on Kodak Industrex Instant 600 paper using a Faxitron 804 X-ray unit and an exposure of 360 mA at 12.5 Kv for two minutes.

It was observed from study 2 that pollen is required for ovule and megagametophyte development. If the ovule does not receive pollen it does not develop and remains as a small rudimentary structure (Fig. 10c). If the ovule is pollinated it continues development but may abort at several stages after pollination resulting in partially developed or full-sized but flat seed (Fig. 10b). Embryo abortion late in development may result in a full-sized, empty, round seed (Fig. 10a). Successful embryo

development results in full-sized, round, filled seed (Fig. 10a). Based on this information, the pollination efficiency (PEF), or the proportion of ovules that receive pollen in their micropyles, was determined by the total number of full-sized round and flat seed plus the partially developed seed (seed class 1 and 2) and divided by the seed potential (SP) per cone. SP is the sum of all three seed classes. SEF was calculated by dividing the filled seed by SP per cone.

Study 2: Six 6 to 7 year-old, 1 m tall, containerized clones consisting of 2 to 3 rooted ramets each were used. Three to five branches per clone bearing a minimum of 25 seed cones were isolated in mid-February before the cones opened. Approximately two-thirds of the cones on six of the clones (231, 258, 683, 696, 708, 713) were pollinated twice with unrelated pollen, two days apart after pollination drops were visible (stage 3) using the same pollination technique as described in study 1. The remaining one-third of the cones were unpollinated. On other ramets of clones 231 and 708, one-third of the cones were pollinated twice with self-pollen, one-third with cross-pollen and one-third left unpollinated. Only 2 clones were self-pollinated because of the limited amount of pollen available from the small ramets. Due to the availability of more cones in clone 708, an additional cross was conducted where the cones in one bag were pollinated only once. The cross pollen was the same polymix from mature trees used in study I. Pollen was fresh and not stored.

Seed cones were collected biweekly from the self, cross and unpollinated cones of clones 231 and 708 and from the cross and unpollinated cones of clones 258 and 683 starting just before pollination in early March until cone maturity in late July. Small cones were sliced longitudinally and the central portion fixed. Developing seeds were dissected from older cones, sliced down one side and fixed. All specimens were fixed in Navashin's chromic acid-acetic acid-formalin (CRAF) solution (Berlyn and Miksche 1977), dehydrated in a tertiary butyl alcohol series of solutions (Johansen 1940), embedded in Tissue-prep, serially sectioned at 8 m and stained with safranin and hematoxylin for microscopic examination.

The number of cones, and later, ovules fixed allowed for about 15 ovules per week to be observed from each of 10 treatments, representing 2 self-, 4 cross- and 4 unpollinated clones. The number of observations per clone or treatment per week was not constant because of the varying frequencies of ovule and cone abortion. About 1470 sectioned ovules were studied anatomically collected from early March to late May, to determine the total number of pollen grains per micropyle, the average number of germinated pollen per micropyle and proportion of germinated pollen. The number of micropyles examined varied from 141 to 182 per treatment. Approximately 276 healthy unaborted ovules were studied anatomically shortly after fertilization to determine the fertilization rate in pollinated ovules. A total of 1960 ovules and developing seed were studied anatomically from early March to late July. For each ovule, the stage of development was recorded by treatment and date of collection. For each

group of collection dates, representing a stage of development, the proportion of degenerating or aborted ovules was tabulated.

The remaining cones were collected at maturity in mid-August. For each clone and pollination twenty cones were randomly selected. For each cone the number of fertile scales, round, flat, underdeveloped and filled seed were determined. From this data SP, FS, PEF and SEF were calculated as previously described.

Study 3: Twenty four 6 to 7-year-old, 1 m tall, containerized clones consisting of 1 to 3 rooted ramets were used. The trees were maintained in a covered shadehouse during pollination. During natural pollen shed, a pollen cloud was raised over the trees by shaking the ramets every two days until all the pollen was shed. Clones that were represented by at least two ramets were used to determine the influence of carrying capacity on the number of fertilized ovules which developed to maturity (filled seed). Three-quarters of the developing seed cones were removed from one ramet per clone, 1 week after cone closure, reducing the average number of cones per ramet from about 1600 to 400. The remaining cones were evenly distributed throughout the crown.

In the fall, all cones per ramet were collected and counted. A subsample to 40 cones per ramet was randomly selected. For each cone/ramet/clone, SP, FS, PEF and SEF was calculated as previously described.

RESULTS

Study 1: Pollination Mechanisms

Considerable variability in seed-cone phenology was observed both between and within the clones. The time between cone opening (stage 2, Figs. 2, 3) and cone closure (stage 5) of unpollinated cones ranged from 15 to 20 days. Pollination drops (stage 3, Figs. 4-8) were usually observed 3 to 6 days after the cones opened and until cone closure if the cones remained unpollinated. In pollinated cones, seed-cone phenology was accelerated. Cone closure (stage 5) was attained 4 to 5 days after pollination, regardless of the stage when pollination occurred. The presence of pollen (Fig. 7) stimulated the drops to recede (Fig. 8), followed by enlargement of the bract-scales and subsequently cone closure. Whether a minimal number of micropyles had to receive pollen before cone closure occurred was not determined.

Pollination drops continued to be exuded in unpollinated cones even after bract-scales began to swell (stage 4). Pollination drops could often be seen oozing from between the bract-scales of unpollinated stage 5 cones even though the ovules were no longer visible.

Effect of Time of Pollination on Cone Length

The phenological stage at which cones were pollinated influenced final cone length (Table 1). If

pollinations were conducted after cone closure (stage 5), when it was not possible for pollen to be taken into the micropyle, all cones remained underdeveloped (cone class 3, Table 1). Twenty-one percent of the cones that were pollinated at stage 1 (clone 720) were partially developed (cone class 2, Table 1). Dissection of these cones revealed, at least one developed or partially developed ovule (seed class 1 or 2) per cone.

The greatest proportion of cones over 1 cm (class 1) and the least number of underdeveloped cones (class 3) were found when pollinations were conducted during stages 2 and 3 (Table 1). For both clones, once the bract-scales started to expand (stages 3-4 or 4), the number of class 1 cones decreased and class 3 cones increased (Table 1).

If stages 1 and 5 are excluded, then clone 653 had proportionally more cones in classes 1 and 3 than clone 720, where most of the cones were found in the intermediate class 2.

Effect of Time of Pollination on SP, PEF and SEF

The phenological stage at which cones were pollinated had no effect on seed potential (SP) per cone (Table 2). The phenological stage of the cones at pollination influenced the average number of pollinated ovules per cone (POV) and subsequently PEF (Table 2). For both clones, the number of pollinated ovules per cone (Table 2) and therefore, PEF (Table 2, Fig. 11) were maximal during stages 2 and 3, then decreased once the bract-scales began to expand (stages 3-4 or 4) and cover the ovules. POV and PEF were zero following the pollination of stage 5, or closed cones (Table 2 and Fig. 11).

Contrary to expectations, the phenological stage at which cones were pollinated (between stages 2 and 4-5) did not affect filled seed (FS) or SEF (Table 2). A high PEF did not guarantee a high FS or SEF (Table 2). In clone 653, the average filled seed per cone ranged from 0.9 to 1.5 when pollinations were conducted between stages 2 and 4-5, even though PEFs ranged from 14 to 50% (2 to 8 pollinated ovules per cone). This corresponds to average SEFs ranging from 6 to 11%. In clone 720, 0.1 to 0.2 filled seed per cone was found when pollinations were conducted between stages 2-3 and 4-5, even though PEF ranged from 10 to 38%.

Relationship between cone length, PEF and SEF

The cone length (cone class) was related to POV, PEF, FS and SEF, ie. the larger class 1 cones contained a greater proportion of ovules with pollen and a higher filled seed rate, than the smaller class 2 cones (Table 3). Class 3 cones had zero POV, PEF, FS and SEF values. When clone 653 was compared to clone 720, the POV and PEF values for the different cone classes were similar. Average pollination efficiencies of 50% were found in all class 1 cones, while PEF values for the class 2 cones were 22 and 16%, respectively. This was not true for FS and SEF where both values were higher in clone 653 than in clone 720 (Table 3).

Additional information was obtained during removal of seeds from individual cones. If

pollinations were made at stage 2, most of the filled seeds were between the upper bract-scales. When pollen was applied after bract-scales began to expand (stage 4) most of the developed seeds were in the basal regions of the cones. These observations indicate that cone closure and receptivity occurred basipetally - the last ovules to be receptive were in the basal region of the cone.

Study 2: Effects on pollen germination

The percentage of micropyles with pollen in cross- and self-pollinations ranged from 61.5% to 91.8%, respectively (Table 4). Cross-pollinated clone 258 was an anomaly with only 19.1% of micropyles containing pollen, possibly because of the stage at which pollinations were made. Excluding this clone, about 75% of the self- and cross-pollinated ovules contained pollen in the micropyles compared to about 4% in 'unpollinated' clones. The latter resulted from failure to remove a few bisporangiate cones from branches within some pollination bags or perhaps very early-arriving pollen that may have adhered to foliage before branches were enclosed in pollination bags.

The average number of pollen grains per micropyle was high, averaging 3.4 in self- and 3.3 in cross-pollinated clones. As many as 8 pollen grains were observed in some micropyles. The average percentage of pollen germination in the micropyles was low, 37.5% in self- and only 8.7% in cross-pollinated clones (Table 4).

Ovule, embryo and seed development in pollinated cones

Although the number of cones or ovules fixed for anatomical study allowed for about 15 observations per treatment per clone each week, the number of observations varied and generally decreased during the study in some treatments more than in others because of ovule and cone abortion. The phenology of ovule and seed development and the proportion of ovules lost at each stage are shown in Table 5. Many of the estimates of times of early abortion are based on degenerated ovules that fixed poorly. It is difficult in these to distinguish degenerating and poorly fixed ovules, therefore, proportions given are approximate but indicate the general trend of development and time and rate of loss of fertile ovules. Table 5 shows the cumulative number of ovules observed and aborted (either degenerating or aborted at some earlier stage) for six collection periods.

The phenology of self- and cross-pollinated cones was similar (Table 5), although the rate of ovule loss varied somewhat with treatment and considerably between clones. On the first collection date (March 4), ovules were at either the pre-meiotic (Fig. 12) or meiotic stages (Fig. 13). These are not included in Table 5 because no abortion was observed at this stage. By the first group of collection dates (March 10 to 28), 42% of ovules sampled were undergoing meiosis (M), 39% were at the megaspore stage (MS) (Fig. 14) and 19% had begun free nuclear division (FN) (Fig. 17). During the next 2.5 weeks essentially all ovules completed meiosis and by the second collection period (April 3 to

24), 87% of ovules were in the FN stage (Fig. 17) and 13% were at the MS stage (Fig. 14). Pollen tubes were found penetrating the nucellus in early April (Fig. 15). About 10% of ovules began to abort at the MS and early FN stages. All megaspores degenerated rather than only the distal three resulting in a dark mass in the centre of the ovule (Fig. 14). These small ovules rarely enlarged after this stage. Ovules were predominantly in the FN stage (Fig. 17) for about 6 weeks, until mid-May. Most of the abortion during this period did not occur until later FN stages (Fig. 18). During the first half of FN (Fig. 17) less than 3% of the ovules aborted. By the third collection period (May 1 to 15) abortion occurred in about 30% of the ovules and increased to about 50% of ovules by the fourth collection period (May 21 to June 5) (Table 5). Abortion at the FN stage was gradual and often difficult to detect because this stage fixed poorly. It appeared that development slowed and the irregular female gametophyte collapsed and slowly degenerated (Fig. 19) but many never totally aborted. These were still recognizable in ovules collected in July from nearly mature cones (Table 5). Ovules in which the later FN stage became arrested (Fig. 19) often became nearly full-sized but were usually flatter than filled seeds, whereas other ovules which aborted at an earlier FN stage (Fig. 17) remained small and the contents were mostly degenerated. These may not have been recognized as the FN stage in later collections. Occasionally the free nuclear female gametophyte aborted, the nucellus proliferated completely filling the seed coat and its cells enlarged often becoming tannin-filled (Fig. 20). This yielded a normal-looking, round, filled seed that lacked both female gametophyte and embryo.

Late in May the stages observed on any one collection date became more variable. Cell wall formation (CW) began in the female gametophyte (Fig. 21) followed rapidly by the central cell stage (CC) (Fig. 22) which lasted about 1-2 w. The mature female gametophyte (MF) (Fig. 23) formed by early June (Table 5). The proportion of aborted ovules was high at this time (between 30-50% of ovules sectioned). Many of these were ovules that had aborted earlier in development at the MS or FN stage. A high proportion of ovules aborted at the CC (Fig. 22) and MF (Fig. 23) stages but few at the cell wall (CW) formation stage (Fig. 21, Table 5). Fertilization occurred during the first week of June. The proembryo (PE) stage (Fig. 24) was brief and by mid-June about 40% of ovules sectioned were at an early embryo stage (Fig. 25). A high proportion of the early embryos aborted (Fig. 26) during the fifth collection period (June 12 to 26) in both self- (28%) and cross-pollinated (19%) ovules (Table 5). Ovule or embryo abortion was not observed after the early embryo stage was completed late in June. No abortion was observed during late embryo development (Fig. 27) in the sixth collection period (July 3 to 27). However, many ovules collected during this time had aborted at earlier, often recognizable stages (Table 5).

Self- and cross-pollinated clones had essentially the same phenology, times at which the highest rates of abortion occurred and percentage of ovule loss through the May 1-15 collection. Thereafter,

the percentage of ovule loss was less in self- than in cross-pollinated clones although the phenology remained similar (Table 5). Numbers for selfed clones are less because only half the number of ramets, thus cones collected, were used. Therefore, the record of times of ovule abortion after early June was less complete in selfed clones than in cross-pollinated clones (Table 5). The expected higher percentage of early embryo (E) abortion in selfed clones (28%) was surprisingly low when compared to crossed clones (19%). Most of the abortion was found in one of the selfed clones.

Phenology and loss of ovules in unpollinated cones.

In the first collection period half of the ovules were undergoing meiosis and half were at pre-meiosis. Meiosis was complete by late March, with 80% of the ovules reaching FN during the second collection period. During April, an average of 13% of the ovules were aborting, mostly at the MS stage. In May the proportion of ovules that were lost increased to 96% and remained at about this level thereafter (Table 5). Most of these aborted at the FN stage.

Effects on Fertilization Rate

By the time fertilization occurred it was obvious that ovules which contained no pollen in the micropyle failed to develop and remained as small rudimentary structures. Ovules which contained pollen in the micropyle developed to the mature female gametophyte stage with many egg cells within the archegonial complex (Fig. 23). In self-pollinated ramets, 61% of all ovules with pollen were successfully fertilized. There was considerable variation in the percentage of fertilized ovules in the cross-pollinated ramets ranging from 7% in clone 258 to 46% in clone 708 averaging 32% for the 4 clones (Table 6).

Effects on SP, FS, PEF and SEF

The SP was essentially the same for all clones, averaging about 14.5 ovules per cone (Table 7). The number of cones sampled varied because of the abortion or poor development.

The self-pollinated clones produced the highest average FS (3.9/cone), PEF (79.7%) and SEF (29.2%). Cross-pollinated clones produced less FS (0.9/cone), PEF (59.5%) and SEF (5.7%). Unpollinated cones produced few seed due to pollen contamination. Cones in clone 708 which were pollinated once had lower average FS, PEF and SEF than cones pollinated twice (Table 7).

Summary of factors affecting seed yield

The different stages influencing final seed yield for the selfed and crossed clones is summarized in Fig. 28. Lack of pollen in the micropyles accounted for a 17% reduction in final yield after selfing and 38% reduction in the cross-pollinated ramets. Pollen inviability or low pollen vigor resulting in no fertilization accounted for a 32 and 42% reduction in final yield in the self- and cross-pollinated ramets, respectively. The SEFs after self- and cross-pollination were 29 and 6% respectively. Other causes including ovule abortion and embryo degeneration accounted for approximately 22 and 14% of the reduction in final seed yield in the self- and cross-pollinated ramets, respectively.

Study 3: Carrying capacity or the number of cones per ramet had no effect on SP, FS, PEF or SEF. No differences were observed in these values whether the ramet carried 1600 cones or 400 cones. The average SP, FS, PEF and SEF per clone is presented in Table 8. Average SP ranged from 13.4 to 15.9 ovules per cone, averaging 14.3 for the 24 clones. Average FS ranged from 0.8 to 5.4 seeds per cone, with an overall average of 3.4 seeds. The highest recorded filled seed per cone was 10. Average PEF ranged from 19.1 to 73.7% per cone, with an overall average of 51.6%. In a few cones 100% PEF was found. Average SEF ranged from 5.6 to 36.7% per cone, with an overall average of 24.2%.

DISCUSSION

The pollination mechanism in western redcedar is well adapted to a long period of pollen shed and seed-cone receptivity. Western redcedar pollination is similar in most respects to *Chamaecyparis nootkatensis* (D. Don) Spach (yellow cedar), the only other member of the Cupressaceae in which the phenology of the pollination mechanism has been studied in detail (Owens *et al.* 1980). In both species pollination drops are exuded from the ovules over many days and if the cones remained unpollinated, this time may be doubled. In the western redcedar most potentially fertile ovules secreted pollination drops at the same time, whereas in yellow cedar there was considerable variation between ovules in the onset of pollination drop secretion. In both species, pollen reaching the seed cone before pollination drop secretion adhered to the ovule tip or more commonly to the bract-scale and some infrequently entered the micropyle. Pollen adhering to the ovule tip or bract-scale may be picked up by the pollination drop, especially in western redcedar where ovules rest deeply between the abaxial and adaxial bract-scales. Observations in this study and an earlier study of yellow cedar (Owens *et al.* 1980) showed that the very large pollination drops exuded from the micropyle commonly wet a large surface of the abaxial and adaxial bract-scales. This large drop could effectively pick up pollen adhering to these surfaces. These surfaces are very smooth and lack hairs or long epicuticular wax rodlets, which might entrap pollen (Owens and Molder 1980). This allows pollen to easily funnel down to the axillary ovules and pollination drops. These features may explain why the PEF at the pre-pollination drop stage (stage 2) was equal to that when pollination drops were present.

Pollen touching a pollination drop was rapidly taken into the drop. Pollen taken into the micropyle either adhered to the micropylar canal or was carried to the nucellar tip. Unpollinated ovules retained visible pollination drops for up to 3 weeks in western redcedar. Natural pollination of western redcedar occurs very early in the season (late winter) In most of its natural range (Fowells 1965) this would insure high humidity and frequent rainfall. Both would increase the size and longevity of pollination drops and maximize the uptake of available pollen, even though rain would greatly reduce the amount of pollen released and reaching the seed cones (Whitehead 1983).

Greenwood (1986) demonstrated in loblolly pine (*Pinus taeda* L.) that rainwater joins with and greatly increases the size of pollination drops facilitating pollination. A similar process may occur in western redcedar.

Pollination of ovules affects the development of the cones in western redcedar. Although bract-scales did swell and cones close in unpollinated cones, the rate of cone closure and development was much slower in the unpollinated cones. This prolonged the period of cone receptivity in the absence of pollen, thus increasing the chance for pollination when little pollen was available. We were unable to determine the number of ovules that must be pollinated before closure is hastened. However, the range in stage of cone closure commonly observed on open pollinated cones suggests that the more ovules pollinated the more rapidly cones close. This feature may enhance seed production by sealing off and protecting ovules soon after the cone is pollinated. The amount of pollen required per ovule in order to induce cone closure was also not determined.

Results from this study indicate that pollination is necessary for normal ovule development. Data from the PEF and cone length portions of the study indicated that the times of pollination that resulted in higher PEF had larger cones and a greater number of full-size seed. This may provide useful criteria for cone collection and sorting in western redcedar. Generally class 1 cones (> 1 cm) have the greatest number of full-size seed (seed class 1 and 2) and the small class 3 cones (< 0.5 cm) had no full-size seed. Unfortunately, full-size seed (high PEF) does not mean high SEF because other causes may reduced SEF. In study 2 the rate of pollen germination in the micropyle using the pollen polymix used was found to be less than 9%. This helps explain why SEF was low for all pollination times despite high PEF. Low seed production/cone (less than 2) may not be because of the absence of pollen but more commonly due to low pollen viability or vigor. High PEF may correlate with cone length but not SEF because pollen may not need to be alive to stimulate ovule and cone development in western redcedar.

PEF was lowest in study 1 (averaged about 40% during stages 2 and 3), intermediate in study 3 (averaged 51%) and highest in study 2 (averaged 70%). The lower levels in study 1 probably resulted from the single pollination given. In study 2, two pollinations, several days apart during stages 2 and 3 increase the overall PEF but not number of pollen grains per ovule. Under open pollinated conditions (study 3) pollination would have occurred over many days. This supports the concept in western redcedar that multiple pollinations are more effective than one and once pollen is taken into the ovule, pollen arriving subsequently will not be taken in, ie. the second pollination increased the number of ovules with pollen but did not increase pollen per ovule.

The SEF and filled seed/cone were lowest in study 1, intermediate in study 2 and highest in study 3. The low levels in study 1, probably resulted from low PEF values. The main difference between study 2 and study 3 was that in study 2, pollen was collected, stored and applied artificially while study

3 was open pollinated where the pollen shed naturally. The polymix used in studies 1 and 2 had a germination rate of less than 9%. While germination rates were not determined for the pollen used in study 3, the fact that about one-half of all pollinated ovules (PEF = 52%) produced filled seed (SEF = 24%), suggests that the pollen had a higher viability rate. Since the pollen used in studies 2 and 3 came from different sources it is not known whether the lower viability of the polymix used in study 2 was due to collection, extraction and storage procedures, or if it was an inherent problem in the pollen. Further research is required in this area.

These studies demonstrate that in seed orchards single controlled pollinations will not be sufficient. From these observations it may be concluded that multiple pollinations (eg. 4/wk) could significantly increase PEF and SEF in western redcedar. Similar recommendations have been made for *Pinus* (Owens *et al.* 1981) and *Picea* (Owens and Blake 1984; Owens *et al.* 1987) in which all ovules are not receptive at once and pollination drops are exuded over several days.

Low seed production/cone in western redcedar in these studies can be explained by a pollination mechanism which is not suitable for single pollinations and the high percentage of dead pollen or pollen of low vigor. In nature low seed/cone in western redcedar is compensated by prodigious cone production.

The large number of ovules (1960) observed in study 2 gives a clearer picture of when seed losses occur. Summary Figure 28 demonstrates that the primary causes of low SEF is the pollination of only a few ovules per cone and poor pollen germination in the pollinated ovules. Observations from the developmental portion of this study of self-, cross and unpollinated clones showed that ovules which contained no pollen failed to develop and aborted primarily at the MS and FN stages. Ovules containing nonviable pollen aborted at any time from MS to MF stages. About 14% of the cross-pollinated and 22% of the self-pollinated ovules did not form filled seed and this could not be attributed to no pollination or no pollen germination. These ovules aborted usually during the FN to early embryo stages and are designated in Fig. 28 as due to other causes. Ovules which aborted at the MF and early embryo stages were usually recognizable because the female gametophyte did not totally degenerate. However, it could not be determined in those that aborted during late FN through CC at just what stage degeneration began or abortion was complete.

It was difficult to determine the relative importance of the different factors under "other causes" (Fig. 28) because although death of the tissue may be abrupt the degeneration of the tissue to the extent that it becomes anatomically recognizable is usually a gradual process. Consequently, although the female gametophyte may die quite early (at MS or FN) it may take several weeks before these ovules appear anatomically different from developing ovules. This is especially true during the long FN stage. The proportion of potential seeds left after those lost due to no pollination or nonviable pollen is often about equally divided between filled seed and seed lost due to abortion during some

stage of development.

Results from the present study demonstrate that pollen is essential for normal female gametophyte and ovule development which in turn is essential for cone enlargement in western redcedar. The absence of pollen within the cones caused ovules to abort at the MS or FN stages and development did not progress beyond the FN stage. Underdeveloped ovules remained small and many degenerated, consequently the numbers of ovules allowing good sections for microscopic examination decreased at later dates. The few ovules that did develop in 'unpollinated' cones were those in which some bisporangiate cones were accidently left in the pollination bags. Even with the limited pollen availability, some of the ovules developed normally and embryos formed. Pollen viability and vigor in turn influence fertilization and SEF.

Viable pollen is not essential for ovule development as indicated by the low percent germination of the polymix used in the cross-pollinated ramets. Although pollinations were not made with killed pollen, clones in which PEF was high but pollen viability was low (low number of germinated pollen per micropyle), had low SEF suggesting that inviable pollen will promote ovule development as in some hardwoods (Stettler 1968) even though fertilization did not occur. If pollen is not present in the micropyle, the ovules remain small and rudimentary and are seen as small undeveloped seed in mature cones.

An earlier study (Owens and Molder 1980) recognized a high proportion of apparently dead pollen in mature microsporangia of western redcedar but the cause was not determined. Selection of clones with a high pollen viability as male parents would greatly increase SEF. The low pollen viability and its potential causes, and a rapid method of screening pollen will be described in a subsequent study.

Our results indicate that selfing in western redcedar may not be as detrimental to SEF as in most other conifers (Owens and Blake 1985). In fact, SEF was as high in selfed clone 708 and much higher in selfed clone 231 than the average for cross-pollinated clones. However, we do not know if pollen viability of the polymix used in the crosses were the same viability of the self pollen. The self-pollinated ovules had a slightly higher embryo abortion than the cross-pollinated ovules which indicates only a weak self-inviability reaction. In other conifers there is a dramatic reduction in SEF after self-pollination, because of embryo abortion which is believed to be due to the action of recessive homozygous lethal alleles (Orr-Ewing 1957; Griffin and Lindgren 1985). Selfing may not be as detrimental to SEF as in other conifers because few genetic polymorphisms have been observed in western redcedar. Copes (1981) found little or no variation in the band patterns of nine enzymes of newly germinated western redcedar seedlings from Oregon and Washington. Von Rudloff and Lapp (1979) observed no differences in leaf oil terpene composition within and between coastal and interior populations and only slight differences between the most widely separated populations. It is quite possible that some clones of western redcedar have a high level of self-fertility. In this study clone 231

was self-fertile while clone 708 displayed the more typical self-infertile reaction. More clones would have to be analyzed to determine the effect of selfing on SEF in western redcedar.

CONCLUSIONS AND RECOMMENDATIONS

Western redcedar ovules must be pollinated with viable pollen or they abort usually during early development. If ovules do not develop the cone does not enlarge and may abort. The greatest loss of seeds resulted from a failure of ovules to be pollinated and low percent viability of pollen. Pollinated ovules may abort at any stage of development but it is most common during the long FN stage. Selfing had no detrimental effect on seed set and postzygotic loss of filled seeds due to embryo abortion was no greater in self- than in cross-pollinated clones. Clonal differences occurred in SEF and stages at which seed losses were most common. Clonal differences may also occur in pollen viability.

To optimize SEF in western redcedar several supplemental pollinations should be applied just after cone opening and when pollinations drops are present with pollen of known high viability and if possible using female parents having a history of high SEF.

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Table 1: The effect of seed-cone phenology (STAGE) at pollination on the final cone lengths of two containerized western redcedar clones in 1986. The proportion of each cone class is expressed as a percentage (%) after the actual value.

				CONE CLASS[1]					
	POLLINATION		TOTAL	1		2		3	
CLONE	DATE	STAGE	CONES	No.	(%)	No.	(%)	No.	(%)
653	Feb. 28	2	25	15	(60)	8	(32)	2	(8)
	Mar. 04	2-3	47	26	(55)	20	(43)	1	(2)
	Mar. 08	3-4	127	29	(23)	72	(57)	28	(22)
	Mar. 10	4	46	8	(17)	20	(44)	18	(39)
	Mar. 14	4-5	84	16	(19)	42	(50)	26	(31)
	Mar. 20	5	38	0	(0)	0	(0)	38	(100)
720	Feb. 28	1	33	0	(0)	7	(21)	26	(79)
	Mar. 08	2-3	63	21	(33)	42	(67)	0	(0)
	Mar. 10	3	136	44	(32)	91	(67)	1	(1)
	Mar. 12	4	35	8	(23)	23	(66)	4	(11)
	Mar. 16	4-5	102	12	(12)	75	(74)	15	(15)
	Mar. 20	5	61	0	(0)	0	(0)	61	(100)

[1]Cone class 1 = (> 1 cm);
Cone class 2 = (< 1 cm > 0.5 cm);
Cone class 3 = (< 0.5 cm)

Table 2: The effect of seed-cone phenology at pollination (STAGE) on average seed potential (SP), pollinated ovules per cone (POV), pollination efficiency (PEF), filled seed per cone (FS), and seed efficiency (SEF) in two western redcedar clones in 1986.

CLONE	STAGE	TOTAL CONES	SP	POV	PEF	FS	SEF
653	2	25	14.5 (0.5)	5.8 (0.5)	40 (6)	1.2 (0.5)	8 (1)
	2-3	47	14.7 (0.3)	7.4 (0.5)	50 (4)	0.9 (0.4)	6 (2)
	3-4	127	13.9 (0.4)	2.8 (0.3)	20 (2)	1.3 (0.6)	9 (3)
	4	46	14.0 (0.3)	1.9 (0.3)	14 (3)	1.5 (0.8)	11 (3)
	4-5	84	13.8 (0.3)	2.2 (0.3)	16 (3)	1.4 (0.8)	10 (2)
	5	38	--	0.0	0	0.0	0
720	1	33	14.4 (0.2)	0.2 (0.1)	1 (1)	<.1 (<.1)	<1 (<1)
	2-3	63	14.4 (0.3)	4.6 (0.6)	32 (4)	0.1 (<.1)	1 (<1)
	3	136	14.3 (0.2)	5.4 (0.6)	38 (5)	0.2 (<.1)	1 (<1)
	4	35	14.5 (0.5)	1.9 (0.5)	13 (4)	0.2 (<.1)	1 (<1)
	4-5	102	14.9 (0.4)	1.5 (0.5)	10 (3)	0.1 (<.1)	<1 (<1)
	5	61	--	0.0	0	0.0	0

Note: Mean values are followed by standard errors (SE) where applicable.

Table 3: The relationship between cone length (CLASS), pollinated ovules per cone (POV), pollination efficiency (PEF), filled seed per cone (FS), and seed efficiency (SEF) in two western redcedar clones in 1986.

CLONE	CONE CLASS[1]	TOTAL CONES	POV	PEF	FS	SEF
653	1	79	6.8 (0.4)	50 (4)	2.1 (0.7)	15 (4)
	2	88	3.1 (0.3)	22 (5)	1.0 (0.6)	7 (3)
	3	75	0.0	0	0.0	0
720	1	60	7.2 (0.6)	50 (4)	0.2 (0.1)	1 (1)
	2	80	2.4 (0.5)	16 (3)	0.1 (<0.1)	<1 (<1)
	3	46	0.0	0	0.0	0

Note: Mean values are followed by standard errors (SE) where applicable.

[1]Cone class 1 = (> 1 cm);

Cone class 2 = (< 1 cm > 0.5 cm);

Cone class 3 = (< 0.5 cm)

Table 4: The number of micropyles containing pollen, number of pollen grains per micropyle and amount of this pollen that germinated in self-, cross- and unpollinated cones in four western redcedar clones.

	Clone	Proportion of micropyles with pollen (%)	Avg. No. of[1] pollen grains per micropyle	Avg. No. of[1] germinated pollen per micropyle	*In vivo* percent germination
Self	231	146/159 (91.8)	3.7	1.3	35.1
	708	103/141 (73.0)	3.0	1.2	40.0
	Ave.	(83.0)	3.4	1.2	37.5
Cross	231	128/168 (76.2)	2.9	.1	3.4
	258	33/173 (19.1)	3.7	.2	5.4
	683	139/167 (83.2)	2.5	.4	16.0
	708	123/182 (67.6)	4.0	.4	10.0
	Ave.	(61.5)	3.3	.3	8.7
Unpol[2]	231	9/152 (5.9)	0.05	.04	--
	258	4/163 (2.5)	0.05	.05	--
	708	7/171 (4.1)	0.05	.05	--
	Ave.	(4.2)	0.05	.05	--

[1]Micropyles with pollen.

[2]Pollen resulted from bisporangiate cones occasionally left on bagged branches or early arriving pollen.

Table 5: The phenology of ovule and seed development at six collection periods for self, cross, and unpollinated (Unpol) cones in western redcedar. For each collection period, the total number of ovules observed (No.) at each stage and the proportion of ovules lost (%L) (aborted or degenerated), are shown.

	Stage[1]	March 10 - 28 No.	%L.	April 3 - 24 No.	%L.	May 1 - 15 No.	%L.	May 21- June 5 No.	%L.	June 12 - 26 No.	%L.	July 3 - 24 No.	%L.
Self	M	32	-										
	MS	31	6	16	6	13	100	2	100				
	FN	26	-	84	7	52	10	13	38			6	100
	CW					3	-	5	20	3	100	1	100
	CC							3	67				
	MF							7	29	2	50	10	100
	PE							4	-				
	E							1	-	29	28	23	-
	TOTAL	89		100		68		35		34		40	
	AVE.		2		7		26		34		35		43
Cross	M	88	-										
	MS	71	10	10	-	19	95	27	100	38	100	41	100
	FN	67	-	156	4	150	29	45	78	16	100	7	100
	CW					8	13	23	4	12	100	6	100
	CC							7	29				
	MF							6	33	9	100	25	100
	PE												
	E									31	19	31	-
	TOTAL	224		166		177		108		106		110	
	AVE.		3		4		31		57		76		72
Unpol	M	85	-										
	MS	86	6	30	50	81	100	38	100	56	100	36	100
	FN			134	7	59	90	50	98	26	96	15	100
	CW												
	CC												
	MF											2	100
	PE												
	E									3	33	4	-
	TOTAL	171		164		140		88		85		57	
	AVE.		3		13		96		99		96		93

[1] Key for developmental stages: Meiosis (M); megaspores (MS); free nuclear divisions (FN); cell wall formation (CW); central cell (CC); mature female gametophyte (MF); proembryo (PE); embryo (E).

Table 6: Proportion of fertilized ovules and percent fertilization (%FERT) for ovules with pollen in the micropyle in four self- and cross-pollinated western redcedar clones.

Treatment	Clone	Fertilized Ovules/ Total Ovules	Percent Fertilization
Self	231	27/44	61
	708	20/33	61
	Total	47/77	Ave. 61
Cross	231	7/44	16
	258	1/15	7
	683	16/40	40
	708	23/50	46
	Total	47/149	Ave. 32

Table 7: Final cone lengths (CLASS) for the self, cross and unpollinated (Unpol) cones in six western redcedar clones.

	CLONE	NO. CONES	CONE CLASS[1] 1		2		3	
Self	231	13	12	(92)[2]	1	(7)	0	(0)
	708	336	275	(82)	52	(15)	9	(3)
	Total (Ave)	349	287	(82)	53	(15)	9	(3)
Cross[3]	231	159	108	(68)	48	(30)	3	(2)
	258	282	0	(0)	225	(80)	57	(20)
	683	221	196	(89)	18	(8)	7	(3)
	696	59	33	(56)	19	(32)	7	(12)
	708	205	103	(50)	97	(47)	5	(2)
	713	119	51	(43)	61	(51)	7	(6)
	Total (Ave)	1045	491	(47)	468	(45)	86	(8)
Cross[4]	708	103	9	(9)	85	(82)	9	(9)
Unpol	231	81	1	(1)	6	(7)	75	(92)
	258	77	0	(0)	22	(29)	55	(71)
	696	57	0	(0)	2	(4)	55	(97)
	683	15	0	(0)	0	(0)	15	(100)
	708	107	15	(14)	47	(44)	45	(42)
	713	115	0	(0)	14	(12)	101	(88)
	Total (Ave)	453	16	(4)	91	(20)	346	(76)

[1] Cone class 1 = > 1 cm; 2 = < cm > 0.5 cm; 3 = < 0.5 cm
[2] Proportion of each size class is expressed as a percentage (%) after the actual value
[3] Pollinated twice
[4] Pollinated once

Table 8: The effect of self, cross and no pollination (Unpol) on seed potential (SP), filled seed per cone (FS), pollination efficiency (PEF) and seed efficiency (SEF) in six western redcedar clones.

Treatment	Clone	No. Cones	Avg. SP	Avg. FS	PEF	SEF
Self	231	13	13.2	6.6	87.8 (3)[1]	50.1 (6)
	708	40	14.1	1.2	71.5 (5)	8.2 (1)
	AVE.		13.7	3.9	79.7	29.2
Cross[2]	231	40	15.9	0.8	81.9 (3)	5.6 (0.8)
	258	20	14.4	<.1	23.0 (2)	0.6 (<.1)
	683	38	13.5	2.0	87.2 (4)	14.5 (2.0)
	696	39	16.1	0.1	60.9 (4)	0.8 (0.1)
	708	40	15.0	1.4	45.0 (4)	8.7 (1.4)
	713	40	15.9	0.7	58.7 (4)	4.1 (0.7)
	AVE.		15.1	0.9	59.5	5.7
Cross[3]	708	29	14.6	.6	24.1 (4)	2.5 (0.7)
Unpol	231	7	14.0	<.1	<.1	0.8
	258	20	14.4	<.1	<.1	0.2
	696	2	15.0	0.0	<.1	0.0
	683	15	--	0.0	0.0	0.0
	708	35	14.4	0.6	0.1	4.6
	713	14	12.9	0.6	<.1	0.8
	AVE.		14.1	0.2	<.1	1.1

[1] Standard error shown in parentheses where applicable.
[2] Pollinated twice.
[3] Pollinated once.

Table 9: The effect of wind pollination on seed potential (SP), filled seed per cone (FS), pollination efficiency (PEF) and seed efficiency (SEF) in 24 western redcedar clones.

Clone	No. CONES	SP	FS	PEF	SEF
384	120	15.0 (0.2)	2.9 (0.3)	34.3 (1.8)	19.5 (2.0)
385	40	14.8 (0.3)	4.8 (0.3)	44.2 (3.1)	32.8 (2.8)
407	120	14.5 (0.2)	4.2 (0.5)	49.2 (2.1)	29.8 (4.0)
431	80	14.7 (0.2)	5.2 (0.5)	66.2 (2.9)	35.8 (3.2)
434	80	13.6 (0.2)	5.4 (0.6)	63.1 (2.6)	39.8 (4.4)
435	40	15.9 (0.4)	4.5 (0.4)	53.6 (3.8)	28.6 (5.1)
436	40	14.0 (0.3)	5.0 (0.6)	73.7 (3.2)	36.2 (4.9)
441	80	14.2 (0.2)	2.6 (0.3)	46.7 (2.6)	18.3 (2.5)
444	80	13.4 (0.2)	2.3 (0.8)	45.7 (2.4)	16.9 (2.1)
448	80	13.7 (0.2)	3.0 (0.5)	45.8 (2.9)	22.4 (1.9)
455	80	15.1 (0.2)	4.0 (0.7)	51.7 (2.2)	26.5 (2.4)
456	80	13.5 (0.2)	3.6 (0.5)	56.9 (2.2)	27.1 (2.1)
459	80	13.8 (0.2)	5.0 (0.7)	73.1 (2.2)	36.7 (2.9)
462	80	13.4 (0.1)	1.9 (0.4)	36.6 (2.1)	14.2 (1.3)
470	40	14.2 (0.3)	2.7 (0.7)	33.4 (2.9)	19.3 (2.5)
483	80	13.6 (0.2)	1.5 (0.3)	19.1 (1.2)	11.3 (1.5)
489	80	14.3 (0.3)	3.8 (0.7)	59.2 (2.5)	27.0 (2.6)
491	80	14.3 (0.2)	1.4 (0.5)	38.4 (2.4)	9.9 (1.5)
497	80	15.2 (0.3)	3.1 (1.0)	49.8 (2.5)	20.8 (2.9)
507	120	14.9 (0.2)	2.0 (0.6)	69.9 (1.7)	13.3 (1.7)
508	120	14.3 (0.2)	4.9 (0.7)	64.3 (2.2)	35.1 (2.6)
510	120	14.7 (0.2)	2.8 (1.1)	48.9 (2.4)	18.9 (3.6)
518	120	13.9 (0.2)	4.4 (1.5)	56.4 (2.3)	32.9 (4.8)
732	40	14.3 (0.4)	0.8 (0.3)	52.0 (2.9)	5.6 (1.1)
MEAN		14.3 (0.2)	3.4 (0.5)	51.6 (2.0)	24.2 (1.9)

Figures 1-10. Pollination mechanism in western redcedar.

Fig. 1. Stage 1; unopened, quiescent seed cones collected in January. x3.

Fig. 2. Stage 2; open seed cones before pollination drop exudation. x4.

Fig. 3. Scanning electron micrograph of stage 2 seed cone with outer bract-scales removed showing bract-scales (bs), ovules (o) and micropyle (m). x30.

Fig. 4. Stage 3; open seed cone, receptive with pollination drops (pd). x6.

Fig. 5. Scanning electron micrograph of stage 3 seed cone. x25.

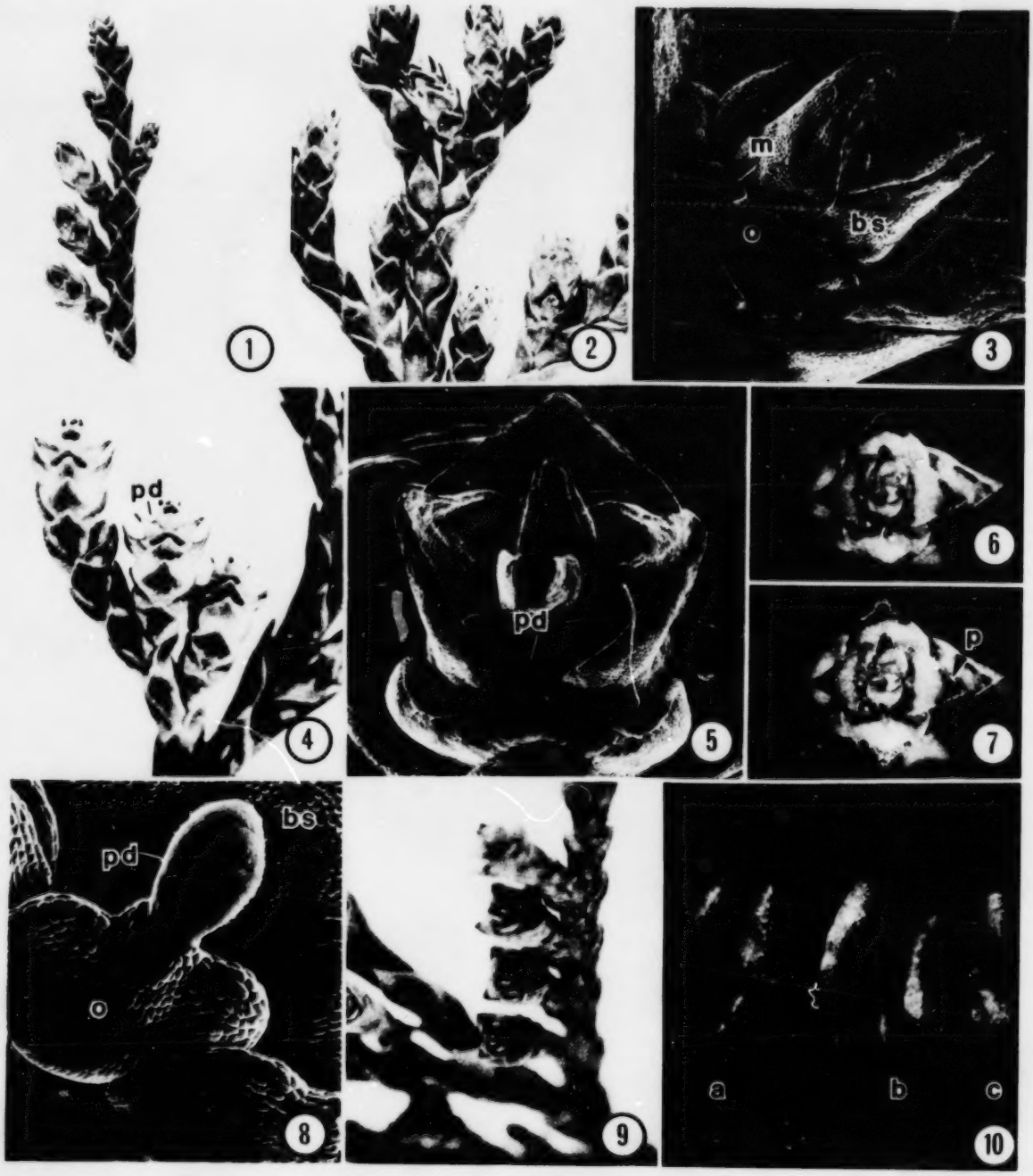
Fig. 6. Light micrograph of stage 3 seed cone before pollen was applied. x20.

Fig. 7. Light micrograph of stage 3 seed cone after pollen (p) was applied. x20.

Fig. 8. Scanning electron micrograph of a portion of stage 3 seed cone showing a large pollination drop making contact with an adaxial bract-scale. x75.

Fig. 9. Stage 4 seed cones as bract-scales begin to swell and cones close. x5.

Fig. 10. The three size classes of seed extracted from mature cones: (a) full-sized round seed; (b) flat or partially developed seed; and (c) small, underdeveloped seed. x8.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c
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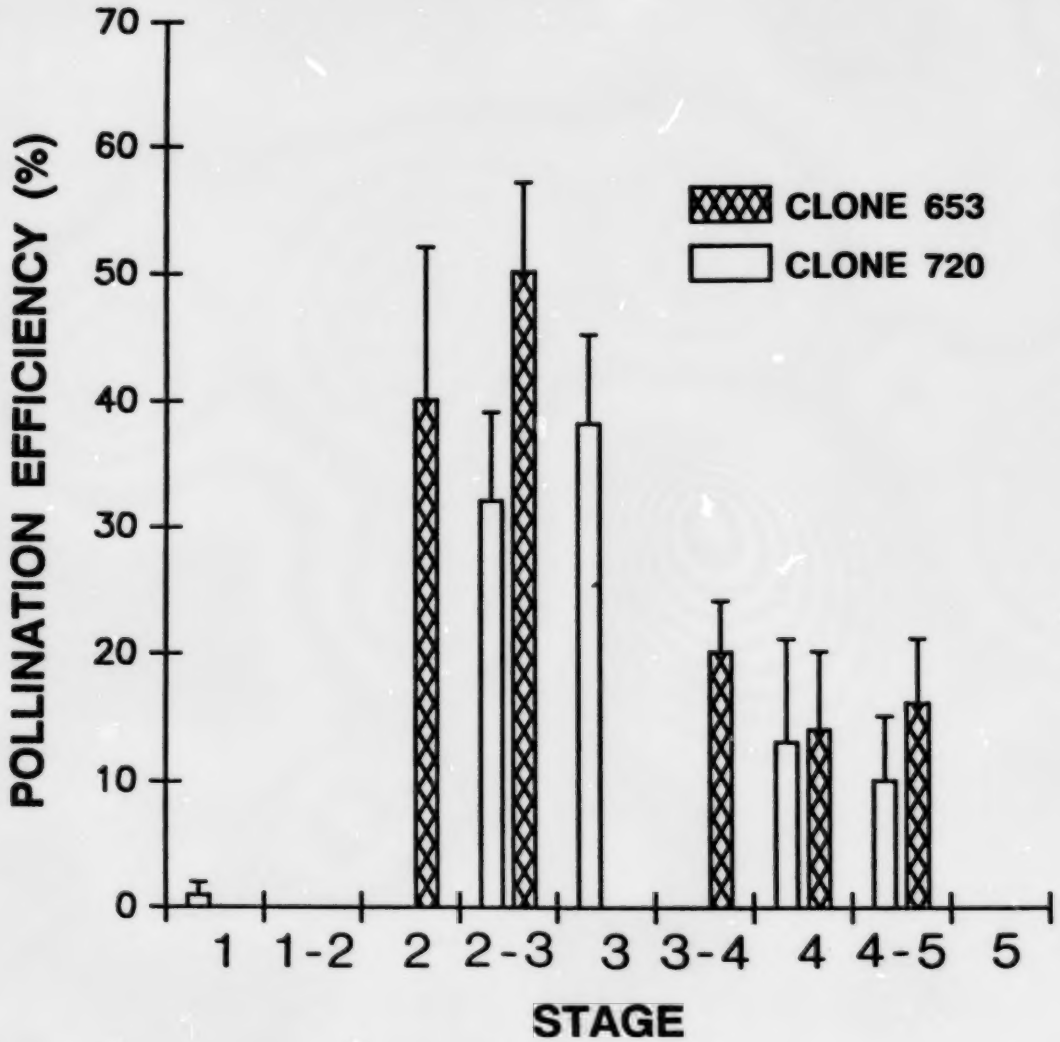
Fig. 11. Pollination efficiency verses phenological stage at pollination for two western red cedar clones. Vertical bars represent standard error.


POLLINATION EFFICIENCY (%)
70
60
50
40
30
20
10
0
CLONE 653
CLONE 720
1
1-2
2
2-3
3
3-4
4
4-5
5
STAGE

Figs. 12-19. Median longitudinal sections of western redcedar ovules.

Fig. 12. Premeiotic ovule showing integument (i), nucellus (n) and megaspore mother cell (mmc). X170.

Fig. 13. Prepollination ovule during meiosis of mmc (arrow). X170.

Fig. 14. Ovule at pollination showing empty secretory nucellar cells (snc) and linear tetrad of megaspores (ms). X170.

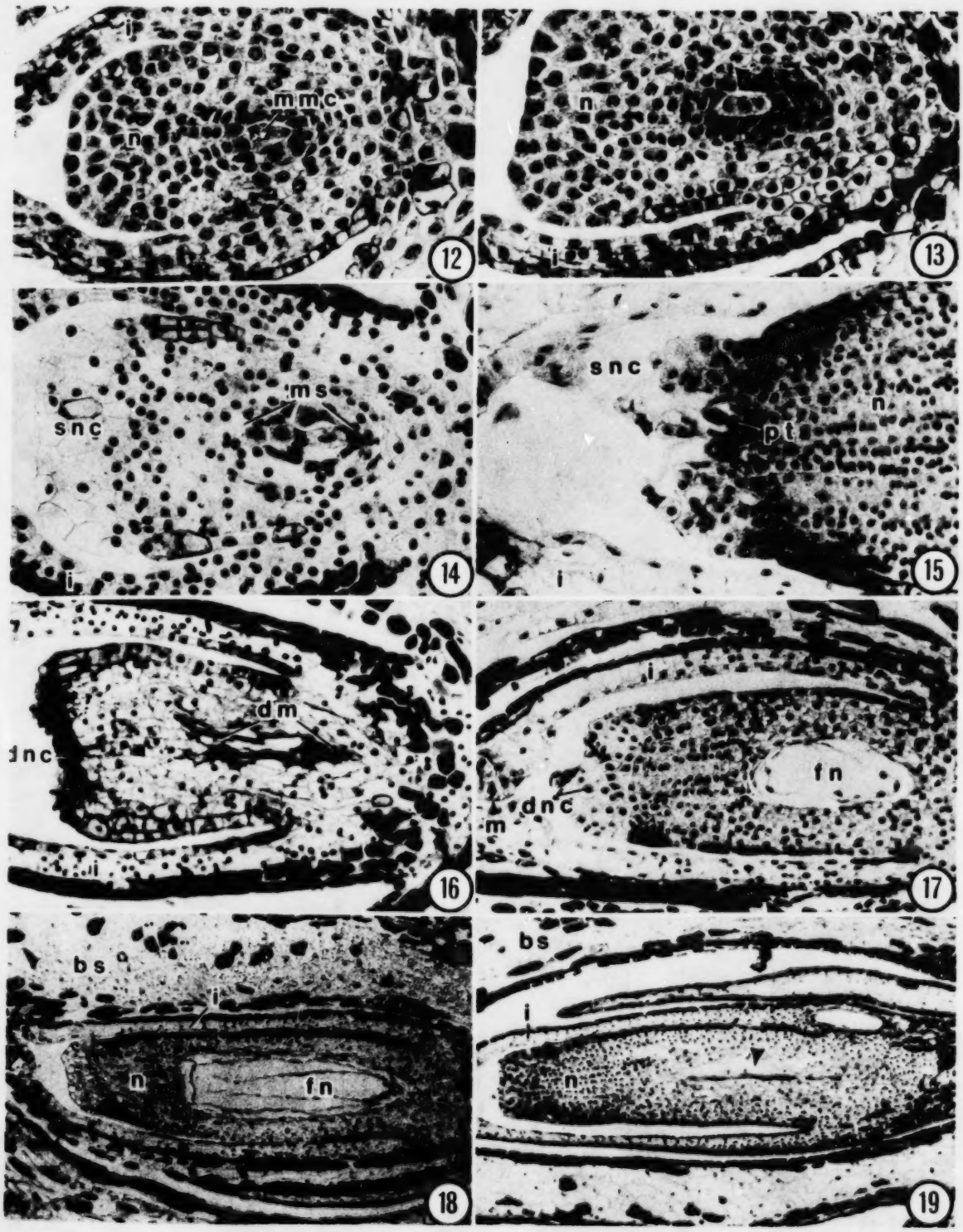
Fig. 15. Nucellar tip containing two pollen tubes (pt). X300.

Fig. 16. Unpollinated ovule showing degenerated nucellar cells (dnc) and degenerated megaspores (dm). X140.

Fig. 17. Early free nuclear female gametophyte (fn) following pollination showing closed micropyle (m). X100.

Fig. 18. Late free nuclear female gametophyte in unpollinated ovule, bs, bract-scale. X55.

Fig. 19. Collapsed late free nuclear female gametophyte (arrow) in unpollinated ovule. X80.


i
mmc
n
12
n
i
13
snc
ms
i
14
snc
n
pt
i
15
dm
dnc
i
16
i
fn
dnc
m
17
bs
i
n
fn
18
bs
i
n
19

Figs. 20-27. Median longitudinal sections of western redcedar ovules.

Fig. 20. Ovule in which the free nuclear female gametophyte has aborted (afn) and the nucellus has proliferated forming a normal-looking seed. sc, seed coat. X100.

Fig. 21. Female gametophyte (mg) during cell wall formation. ai, archegonial initials; n, nucellus, i, integument. X215.

Fig. 22. Ovule at central cell (cc) stage showing a pollen tube (pt) in the nucellus. X70.

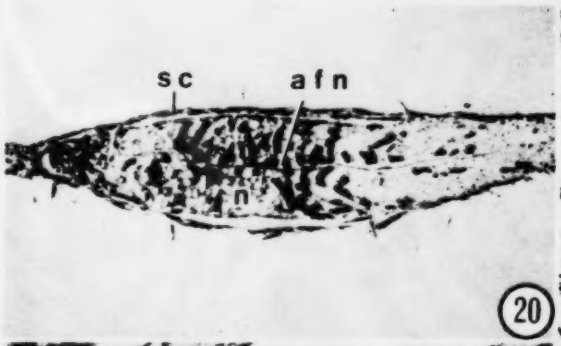
Fig. 23. Mature female gametophyte showing three archegonia (a) in an archegonial chamber. X120.

Fig. 24. Early free nuclear proembryo (pe) stage. X130.

Fig. 25. Early embryo stage showing one aborting embryo (ae) and one developing early embryo (ee). X120.

Fig. 26. Aborted early embryo in degenerating female gametophyte. X120.

Fig. 27. Late embryo development showing a nearly full-size embryo with colytedons (c) within the mature female gametophyte (mg). X65.



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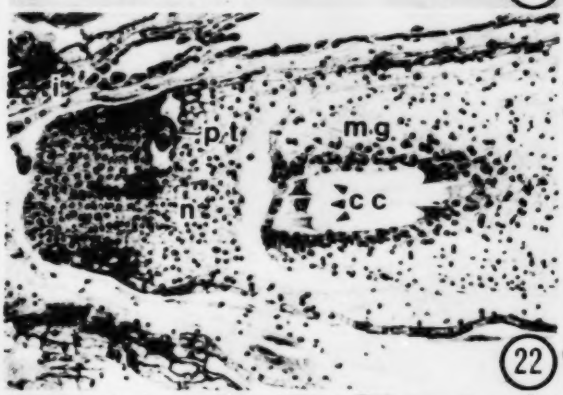

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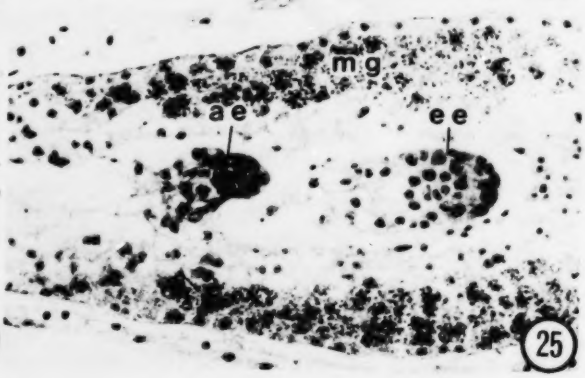

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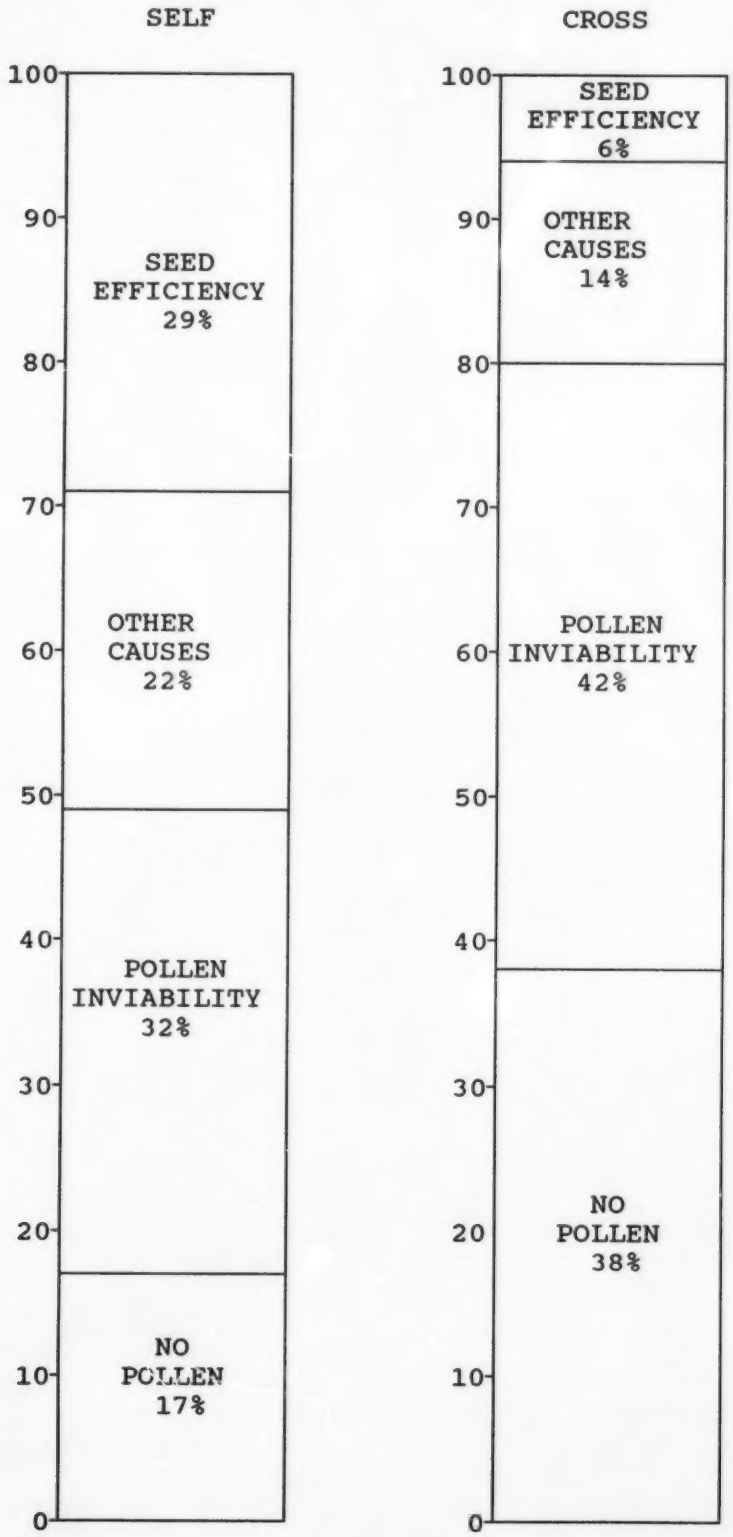
Figure 28: Summary of average percentages of potential seed lost due to various causes and final seed efficiencies for two self- and four cross-pollinated clones of western redcedar.


SELF
CROSS
100
90
80
70
60
50
40
30
20
10
0
SEED EFFICIENCY 29%
OTHER CAUSES 22%
POLLEN INVIABILITY 32%
NO POLLEN 17%
SEED EFFICIENCY 6%
OTHER CAUSES 14%
POLLEN INVIABILITY 42%
NO POLLEN 38%